



MINI-REVIEW

Sound perception and its effects in plants and algae

Francesca Frongia, Luca Forti, and Laura Arru

Department of Life Science, University of Modena and Reggio Emilia, Modena/Reggio Emilia, Italy

ABSTRACT

Life evolved in an acoustic world. Sound is perceived in different ways by the species that inhabit the Planet. Among organisms, also some algal species seem to respond to sound stimuli with increased cell growth and productivity. The purpose of this Short Communication is to provide an overview of the current literature about various organisms and sound, with particular attention to algal organisms, which, when subjected to sound applications, can change their metabolism accordingly.

ARTICLE HISTORY

Received 10 July 2020
Revised 4 September 2020
Accepted 17 September 2020

KEYWORDS

Sound vibration; sound perception; Hertz; algal metabolism

Sound: definition and propagation

Sound is a vibration that propagates in the form of a sound wave through a medium that can be a liquid as water, a gas as air or a solid material.^{1,2} Sound waves are generated by a sound source that creates vibrations in the surrounding medium. While the sound source continues to vibrate the medium, vibrations propagate far from the source at the speed of sound, forming the sound wave.

Sound is transmitted through water and air with longitudinal waves, through solids with longitudinal and transverse waves. In longitudinal waves particles oscillate along the direction of propagation, while in transversal ones the direction of particles oscillation is at right angle to the direction of propagation.

Sound waves are characterized by frequency (Hz), intensity (dB) and timbre, which at the same frequency distinguishes one sound from another. The speed of propagation of sound depends on the characteristics of the medium; in particular, it is directly proportional to elasticity and inversely proportional to density.¹

The frequency bands of naturally audible sound are divided into:³

- low-frequency bands, from 20 Hz to 200 Hz;
- medium-low frequency bands, from 200 Hz to 1 kHz;
- medium-high frequency bands from 1 kHz to 5 kHz;
- high-frequency bands from 5 kHz to 20 kHz.

For frequencies lower than 20 Hz we talk of infrasounds, for those higher than 20 kHz of ultrasound. The sound volume is measured in decibels (dB), perceived in a specific way by our hearing. See below in Table 1 some examples.

The behavior of sound propagation is generally influenced by three factors. The first is the relationship between the density and the pressure of the medium, which is influenced by temperature and determines the speed of sound within the medium. The second is the motion of the medium: if the medium is moving, this movement may increase or decrease

the absolute speed of the sound wave depending on the direction of the movement. The third factor is the viscosity: the average viscosity determines the speed at which the sound is attenuated, but for water or air the attenuation due to viscosity is negligible. In addition, during propagation, waves may be reflected, refracted, or attenuated by the medium.²

When sound propagates in air, high frequencies are absorbed more than low because of the molecular relaxation phenomenon, and the amount of absorption depends on the temperature and humidity of the atmosphere. Precipitation, rain, snow, or fog has an insignificant effect on sound levels although the presence of precipitation will obviously affect the humidity and may affect wind and temperature gradients.⁴

Furthermore, scattering occurs when sound waves propagate through atmosphere and meet a region of inhomogeneity; therefore, some of their energy is redirected into many other directions. In environmental noise, air turbulence, rough surfaces, and obstacles such as trees may cause scattering.⁵

When sound is propagated in water, a distinction must be made between deep water and shallow water. In deep water, the main natural sources of noise arise from waves generated by tidal and wind cycles, seismic disturbances such as earthquakes and volcanism, lightning, rain, ocean turbulence, and marine mammals. In shallow waters, the main natural sources of noise arise from waves hitting the shore, local wind, rain, and biological sounds such as shrimp and marine mammals. Furthermore, account should be taken of anthropogenic noise, such as ship noise, particularly commercial ships, which in recent centuries has increased ambient noise levels at frequencies below 1 kHz. Rain noise is fairly constant on all frequencies, while wind noise is one of the predominant natural factors influencing low-frequency ambient noise levels.¹

Sound perception in humans, animals and plants

In human physiology and psychology, the sound is the reception of sound waves and their perception by the brain. Only waves with frequencies between about 20 Hz (infrasound) and

Table 1. Correlation between sound volume and human perception (modified from <http://salfordacoustics.co.uk/sound-waves/waves-transverse-introduction/decibel-scale>).

Sound	dB	Human perception
Rocket to take off	180–200	Instant damage to hearing
Engine of a plane to take off	140	Painful
Pneumatic hammer	100	Very annoying
High music	90	Very annoying
Heavy traffic	80	Annoying
Normal conversation	60	Moderate
Whisper	20	Tenue
Rustle of leaves	10	Very soft

20 kHz (ultrasound), the range of audio frequencies, arouse an auditory perception in humans. In air at atmospheric pressure, they represent sound waves with wavelengths from 17 m (56 feet) to 1.7 cm (0.67 inches). Different animal species have different auditory ranges.^{6–9} For example, ultrasounds are perceived by some animal species such as dolphins and bats, while infrasounds are perceived by elephants, fish, and cetaceans.

Many species such as frogs, birds, marine and terrestrial mammals, have also developed special organs to produce and receive sounds, and they can detect the sound pressure and the vibration of the particles associated with sound with specific organs (i.e. ears) or with the totality of the body surface (somatic hearing).^{10,11}

Plants communicate both by sending volatile chemical signals and through the network of fungi that intersects their roots.¹² Volatile compounds mediate the interaction of plants with pollinators, other plants, and microorganisms.¹³ There is not much knowledge about sound communication in plants, but it is known that these can produce sound waves at relatively low frequencies such as 50–120 Hz. Plants emit also ultrasonic vibrations of 20–100 kHz, measured by connecting a sensor directly to the stem of the plant.¹⁴ Plants release sound emissions from different organs and at different growth stages or in response to different situations. Through the use of small highly sensitive sound receivers, it has been shown that plants emit sound from the xylem¹⁵ and faint ultrasound in case of stress.¹⁶ Plants can hear caterpillar's chewing and set up the appropriate defenses¹⁷ but they can also hear the moving close of a pollinator using flowers as "ears" and responding with minutes by sweetening the nectar.¹⁸

From several years it has been demonstrated how plants can absorb and resonate specific sound frequencies¹⁹ and how sound waves can change the cell cycle of the plant. Sound waves vibrate plant leaves accelerating protoplasmic movement in cells.²⁰ It is not yet entirely clear the mechanism by which sound intervenes in the growth of plants, although the biological effects of sound have been previously studied. A study found that some stress-induced genes could be activated at the level of transcription under sound stimulation.²¹ The stimulation of sound waves could also increase the plant plasma-membrane H⁺ ATPase activity, the contents of soluble sugars, soluble proteins, and amylase activity of callus.^{22,23} Sound vibrations can influence the rearrangement of microfilaments, increase levels of polyamines and soluble sugars, change the activity of various proteins and regulate the transcription of certain genes.^{24–26}

Recent studies show that plant organisms perceive sound as a mechanical stimulus and translate it into cellular and metabolic changes. Sound stimuli can influence germination rates and increase plant growth and development, improving the yield of

some crops.^{14,25,27,28} Furthermore, sound waves can improve plant immunity against pathogens and can also increase their tolerance to drought.^{29,30} The sound exposure increases the absorption efficiency of the light energy which translates into greater photosynthetic²⁷ Plants can recognize the mating sounds of insect larvae and the humming of a pollinating bee and respond accordingly.^{31,32}

Macroalgae and microalgae

Algae are a heterogeneous group of photosynthetic organisms living in an aquatic environment, classified into two large groups: macroalgae or seaweed, macroscopic, and microalgae, microscopic, and unicellular.³³

Both have important ecological roles in carbon and nutrient cycling, as oxygen producers, as well as food base for almost all aquatic life, but they are also economically important as a source of food and a range of industrial products for humans.

Sound perception in macroalgae and microalgae

Algae interact through sending and receiving chemical signals with individuals of their own species and other species.³⁴ Conspecific interactions are mediated by pheromones, while inter-specific communication involves allelochemicals. Allelochemical interactions may play a role during competition through the production of compounds that suppress other species or may involve mutual relationships in which the release of metabolites promotes the growth of other species. Natural algae products can also act as a defense mechanism against herbivores or mediate interaction with associated microorganisms or pathogens.³⁵ There is not much knowledge about other forms of communication between algae organisms, and the perception of sound in microalgae is an almost unexplored phenomenon.

In a study from 2018, it was observed that seaweed produces sound during photosynthesis. Biological noise results from the formation and consequent release of oxygen from algal filaments. During the release, the oxygen bubble assumes a spherical shape creating a monopolar sound source that is distributed by resonance over the seabed. This phenomenon, ubiquitous but previously neglected, is useful for the quantification of algae both in the ecosystem and at the level of raw materials for industrial production. The results show that algae are able to produce sound under normal circumstances and that sound is produced in the 2 to 20 kHz band.³⁶

The transmission of the mechanical sound stimulus in algal cells involves changes at the cellular level. Some authors state that the possible cause of the alteration of the cellular resonance frequency could be the change of the viscosity characteristics in the fluid inside the cell.³⁷

Cells respond to sound as to mechanical stresses, such as shear stress, changes in plasma-membrane tension, hydrostatic pressure, compression with changes in membrane traffic. The plasma membrane has an associated tension that modulates both exocytosis and endocytosis. As membrane tension increases, exocytosis is stimulated, and endocytosis is slowed down. The decrease in membrane tension stimulates internalization, thereby slowing exocytosis. Secretion is stimulated by external mechanical stresses, although in some cells mechanical forces block secretion.

Transduction of mechanical stimuli in changes in exocytosis and endocytosis may involve the cytoskeleton, stretch-activated channels, integrins, phospholipases, tyrosine kinase, and cAMP³⁸ (Figure 1).

Furthermore, cells respond to external stresses by changing a number of factors including cell division, dimensional growth, signal transduction, gene expression, and membrane ion channel activation.^{39,40} Mechano-sensitive ion channels (MS) are membrane proteins that have the ability to open and close as a result of mechanical forces resulting from gravity, osmotic pressure, and sound. When the ionic channels are in their open state, in response to mechanical forces, they allow the passage of ions, especially Ca^{2+} and K^{+} , through the membrane, in order to originate an ionic current that can become an electrical or chemical signal (mechatronics). The membrane tension generated can be transmitted directly into the channel through the lipid double layer or merge indirectly to other cellular components.⁴¹

Applications of sound in macroalgae and microalgae

To date, there are few application reports regarding the use of sound to promote the growth and productivity of algal organisms.

A study from 2012 involved the microalga *Chlorella pyrenoidosa*: the effects of sound waves on algae propagation were evaluated, in search of the optimal frequency for the promotion of growth. *C. pyrenoidosa* was cultivated for 7 days: several sound frequencies were tested, collecting growth rate data and comparing them with control groups. The experiments showed that the growth of *C. pyrenoidosa* was significantly improved when the microalga was exposed to 0,4 kHz frequency sound waves, with an increase in growth between 12% and 30% compared to control groups.⁴²

In another study, it was reported that the growth stimulus of the microalga *Picochlorum oklahomensis* was higher during the exposure to 2,2 kHz sound frequency.⁴³ Tests were performed at 1,1, 2,2, and 3,3 kHz frequencies. The study highlights as the daily increase in growth rate is major in the exponential phase of microalgae growth. Moreover, cultures exposed to sound

waves took 26 days compared to 30 days in control groups to reach the steady-state growth. The study demonstrates that audible natural sounds improve algal biomass production, considering that 2,2 kHz frequency is the predominant component of most of the sounds we can find in nature. This could be the fundament for the improvement of algal cultures through the use of sound waves in closed cultivation systems such as bioreactors. This research not only evaluates the biomass productivity, but also the lipid yields, proving that sound waves stimulate both microalgae growth and synthesis of valuable cell product of biotechnological interest.

In 2013 it was created a method called “Microbial Bebop.” This method consists in the creation of music using environmental data, starting from observation of natural patterns and taking inspiration from some bebop jazz principles.⁴⁴ The method uses beat, pitch, duration, and harmony to highlight relationships between multiple data types in complex biological data sets. With this data collection, derived from the environmental monitoring station L4 in the Western English Channel, four compositions were generated. Each composition is derived from the same dataset and highlights the relationships between environmental factors and structure of the microbial community, considering different aspects of the ecological interactions of the microbial communities. The compositions created by specific algorithms are “Blues for Elle,” “Bloom,” “Far and Wide” and “Fifty Degrees North, Four Degrees West”. This kind of approach can be applied to a wide range of complex biological data sets. In recent years it was studied the effect of “Blues for Elle” and “Far and Wide” for inducing growth and productivity in microalga *Haematococcus pluvialis*.⁴⁵ The experiment was conducted by exposing the microalga culture at audible sound for 8 and 22 days with an intensity of 60 dB. The results showed an increment in the growth rate of 58% respect to the control without music exposition. The coding in musical synthesis of the ecological data could be exploited for the induction of ecosystems to reproduction and to the synthesis of cellular components of important biotechnological relevance.

It has been confirmed that algae exposed to sound taken as a single frequency/intensity or as a set of different frequencies/intensities respond with an increase in growth rate^{42,43,45} but also with an increase in cellular productivity.⁴³ As in other organisms, the time of exposure to sound should also be considered in algae. In addition, being algae aquatic organisms, it is necessary to consider the aqueous medium in which sound is propagated.

In the case of the *Chlorella pyrenoidosa* microalgae, an improvement in growth was observed at 0.4 kHz,⁴² while frequencies of 10 and 15 kHz, even if increases the photosynthetic pigments biosynthesis, have a general biomass reducing effect in *C. vulgaris*.⁴⁶ Still, irradiation with 5, 10, 15, and 20 kHz frequencies in the same microalgae increases the synthesis of triacylglycerols, suggesting the usefulness of a deeper investigation with the aim of biodiesel production.

In *Picochlorum oklahomensis* the improvement of the growth has been evidenced with an exposure to 41 kHz at 90 dB, to which an increment of the lipidic yield has been placed side by side.⁴³ In the study with the microalga, *Haematococcus pluvialis* was measured that the compositions “Blues for Elle” and “Far and Wide” correspond, respectively, to 0.28 kHz and 0.24 kHz at 60 dB.⁴⁵

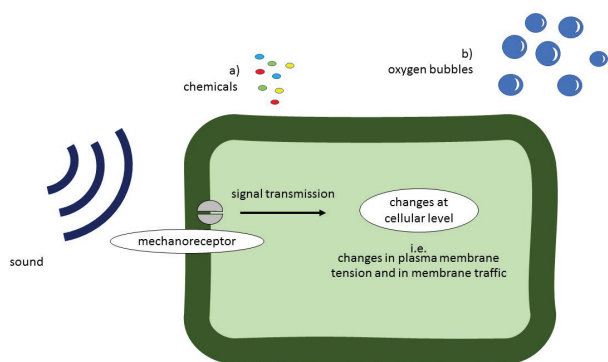


Figure 1. Algal communication. Besides a) pheromones (conspecific interactions) and allelochemicals (interspecific communication), algae can also indirectly produce sound by oxygen bubbles naturally evolving during the process of photosynthesis (b). The presence of mechano-sensitive proteins in the plasma membrane can mediate a sound response influencing changes in hydrostatic pressure, in plasma-membrane tension, and therefore in membrane traffic.

A higher growth rate was observed in microalgae exposed to the higher frequency of “Blues for Elle.”

In the panorama of the application of sound, algae cover only a small part that surely deserves to be further investigated. The frequencies and the intensities useful for the promotion of the growth and the productivity of the algae vary between the different species, and those explored up to now are not sufficient to give a complete idea of the possible combinations.

Sound application in other organisms

There are several studies that report the effectiveness in promoting the growth of organisms exposed to sound stimuli of various nature.

In plants, depending on the frequency or intensity of the sound waves to which these organisms are exposed, it could happen that they will go against both a promotion in growth and a greater resistance to diseases and parasites.^{14,47}

Plant Acoustic Frequency Technology (PAFT) was developed to increase crop productivity and quality through exposure to sound waves. The PAFT technology aims to provide exposure to sound waves in plants at specific frequencies in accordance with the plant's meridian system to increase crop production and decrease use of fertilizers.¹⁴ There are a few studies suggesting that plants might have a meridian system as humans and other animals (that means internal frequency) and that they can vibrate in response to specific external sound frequencies enhancing quality and yield.^{48,49}

Recently, the effect of audible sound has been studied on the germination and growth of the green bean, exposing it for 72 h to a frequency ranging from 1 to 2.5 kHz and with variable intensity (80/90/100 dB).²⁷ The study found a decrease in germination time and a significant increase in the growth of buds exposed to frequencies of 2 kHz and intensity of 90 dB.

In another study, the green bean was grown in open-air chambers under controlled environmental conditions. The beans have been exposed to 5 different types of acoustic patterns (soprano, classic, nature, rock, koranic acting) with 60 dB sound pressure level and with a control chamber without sound exposure. In this case the results indicate that different types of acoustic patterns favored the growth of different parts of the beans, such as stem length, number of leaves, and length of roots. The soprano had a significant effect on the length of the stem, while the Koranic recitation had an effect on the production of leaves.⁵⁰

Recently, the effect of sound exposure on tomato plants (*Solanum lycopersicum*) has been studied.⁵¹ Tomato plants were exposed to three different consecutive frequency values: 0.6 kHz in the first week, 1.24 kHz in the second week and 1.6 kHz in the third week of growth, with a volume of 90 dB. The total phenol content, lycopene content and ascorbic acid of tomato plants exposed to sound waves at different frequencies increased by 70%, 20%, and 14%, respectively. According to the results of all the parameters measured in tomato fruits (lycopene, vitamin C, total sugars, total acids, and total phenol levels), 1.6 kHz was the best frequency value of sound waves.

Some other studies related to the application of sound on the growth and productivity of plants are shown in Table 2.

Table 2. Applications of sound on plants [modified from 15].

Plant species	Sound-exposed tissues	Frequency (kHz)	Intensity [dB]	Duration	Plant responses	Reference
Arabidopsis	Shoot	0,5	80	1 h	Increased expression of defense-related genes	Ghosh et al., 2016
	Shoot	0,5	80	1 h	Increased expression of mechano-stimulus responsive genes	Ghosh et al., 2016
	Shoot	0,25/0,5	80	1 h	Increased expression of photosynthesis-related proteins and genes	Kwon et al., 2012
	Shoot	0,5	80	1 h	Increased expression of redox homeostasis genes	Ghosh et al., 2016
Cotton	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
Cucumber	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
95	1 h	Changes in hormone levels	Bochu et al., 2004		Chrysanthemum	Mature callus 1,4
Stem	1	100	1 h	Increased levels of soluble proteins	Yi et al., 2003	
Lettuce	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
Maize	Root	0,1/0,2/0,3	Unknown	Unknown	Root tip bending	Gagliano et al., 2012
Pea	Root	Unknown	Unknown	Unknown	Root growth toward flowing water	Gagliano et al., 2017
Rice	Shoot	0,125/0,25	65/70	4 h	Increased expression of light responsive genes	Jeong et al., 2008
	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
	Shoot	0,8/1	100	1 h	Enhanced tolerance to drought stress	Jeong et al., 2014
	Shoot	0,8/1	100	1 h	Increased photosynthesis	Jeong et al., 2014
Spinach	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
Strawberry	Shoot	Unknown	Unknown	3 h	Increased photosynthesis	Qi et al., 2010
Sweet pepper	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
Tomato	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014
	Fruit	1	100	6 h	Delayed ripening	Kim et al., 2015
Wheat	Shoot	0,1/1	70	3 h	Increased yield	Hassanien et al., 2014

Hight and low-frequency sonic vibration can also affect growth in yeast cells. In a study carried out by Aggio and colleagues in 2012, differences in metabolic pathways of yeast cells growing in liquid medium exposed to music have been evaluated. The sound stimuli applied were at three different frequencies and intensities: low frequency (100 Hz at 92 dB), high frequency (10 kHz at 89 dB) and broadband (320 kbps at 80/90 dB) compared with silent controls with 90 dB background. The sonic stimuli increased the grown rate of the yeast cells by 12% but they also reduced biomass production by 14%. In this study, it was confirmed that the intra and extracellular metabolite profiles differed significantly depending on the sonic stimulus applied showing that different metabolic pathways are affected differently by different sound frequencies.

The effect of sound waves was investigated in bacteria growth as well. Three types of sound frequencies falling within the audible range were applied in the *E. Coli* strain. The bacteria strain was found to register better growth at a frequency below 1 kHz but was registered an extremely poor growth at a frequency above 1 kHz under the influence of distinctive sound frequencies.⁶¹

As it can be observed from the results presented so far, the panorama of sound applications in organisms is very heterogeneous. Plants exposed to medium/low bands of frequency and intensities result in increased growth rates, photosynthetic rates, and increased pest resistance.^{14,47,52} Changes are also evident at the cellular level in yeasts and bacteria, although in some cases an increase in the growth rate is accompanied by an impoverishment in the biomass content.⁶²

In general, these and other studies mean that the interest in plant acoustic is shifting from “if” plant can sense sound to “how” they can do it. Plants have been exposed to many different (and amazing) kind of sounds, i.e. from Vedic Chants⁶³ to Mozart⁶⁴ to artificial single buzz^{14,18,65,66} to insect recordings [i.e. 17, 18]. The results are always consistent: plants produce secondary defense molecules when subjected to pathogen-related sounds, or grow better with higher yields or related parameters, or germinate earlier, etc. “Why is that” is the new big challenge of the plant acoustic basic research field, too often pushed into the background by the biotechnology application in agriculture.

Conclusions

In the future it will be interesting to deep into the field of acoustic with combined investigation of frequencies and intensities, to understand the molecular/physiological responses with the combination of sounds/algal strains tested so far and different ones.

What is clear is that sound, even frequencies not audible by humans, can affect other organisms, including plants and algae. The first studies will be followed by an in-depth knowledge of the ecological relevance of sound perception and response, and it could happen that, in addition to air pollution, light pollution, and many other forms of human interference in Nature, we should also be careful about noise pollution.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed

References

1. Bass AH, Clark CW. The physical acoustics of underwater sound communication. New York (NY): Springer Handbook of Auditory Research, Springer; 2003. 16.
2. Urlick RJ. Principles of underwater sound. New York (NY): McGraw-Hill; 1983.
3. Rosen S, Howell P. Signals and systems for speech and hearing. Brill Ed.; 2011;29.
4. Ingard U. A review of the influence of meteorological conditions on sound propagation. J Acoust Soc Am. 1956;25:3.
5. Harris CM. Absorption of sound in air versus humidity and temperature. The Journal of the Acoustical Society of America. 1966;40(1):1. doi:10.1121/1.1910031.
6. Hedwig B, editor. Insect hearing and acoustic communication. Heidelberg (Germany): Springer; 2014.
7. Dooling RJ, Popper AN. Comparative hearing: birds and reptiles. Springer Handbook of Auditory Research. New York (NY): Springer; 2000.
8. Fay RR, Popper AN, editors. Comparative hearing: fish and amphibians. Springer Handbook of Auditory Research. New York (NY): Springer; 1999.
9. Grinnell AD. Hearing by bats. Springer Handbook of Auditory Research. New York (NY): Springer; 1995.
10. Manley GA, Vater M, Meng I, Fox RC. Hearing organ evolution and specialization: early and later mammals. Evol Vertebrate Auditory Sys. 2004;9:256–288.
11. Peng AW, Ricci AJ. Somatic motility and hair bundle mechanics, are both necessary for cochlear amplification? Hear Res. 2011;273 (1–2):109–122. doi:10.1016/j.heares.2010.03.094.
12. Song YY, Zeng RS, Xu JF, Li J, Shen X, Yihdego WG, Van der Heijden M. Interplant communication of tomato plants through underground common mycorrhizal networks. PLoS ONE. 2010;5 (10):e13324. doi:10.1371/journal.pone.0013324.
13. Bouwmeester H, Schuurink RC, Bleeker PM, Schiestl F. The role of volatiles in plant communication. Plant J. 2019;100(5):892–907. doi:10.1111/tj.14496.
14. Hassani RHE, HOU T-Z, Li Y-F, Li B-M. Advances in effects of sound waves on plants. J Integrative Agric. 2014;13(2):335–340. doi:10.1016/S2095-3119(13)60492-X.
15. Jung J, Kim S, Kim J, Jeong M, Ryu M. Beyond chemical triggers: evidence for sound-evoked physiological reactions in plants. Front Plant Sci. 2018;9:25.
16. Khait I, Sharon R, Perelman R, Boonman A, Yovel Y, Hadany L. The sounds of plants – plants emit remotely-detectable ultrasounds that can reveal plant stress. Suppl Mat. 2018. doi:10.1101/507590.
17. Appel HM, Cocroft RB. Plants respond to leaf vibrations caused by insect herbivore chewing. Oecologia. 2014;175:1257–1266.
18. Veits M, Khait I, Obolski U, Zinger E, Boonman A, Goldshtein A, Saban K, Seltzer R, Ben-Dor U, Estlein P, et al. Flowers respond to pollinator sound within minutes by increasing nectar sugar concentration. Ecol Lett. 2019;22(9):1483–1492. doi:10.1111/ele.13331.
19. Hou TZ, Li MD. Experimental evidence of a plant meridian system: V. Acupuncture effect on circumnutation movements of shoots of *Phaseolus vulgaris* L. pole bean. Am J Chin Med. 1997;25:253–261.
20. Cai W, Zhu S, Ning W, He H, Ying B. Design of an experimental platform to investigate the effects of audible sounds on plant growth. Int J Agricul Biolog Eng. 2015;8:162–169.
21. Xiujuan W, Bochu W, Yi J, Chuanren D, Sakanishi A. Effect of sound wave on the synthesis of nucleic acid and protein in *Chrysanthemum*. Colloids Surf B Biointerf. 2003;29(2–3):99–102. doi:10.1016/S0927-7765(02)00152-2.
22. Sun K, Xi B, Cai G, Shen Z. The effect of alternative stress on the thermodynamical properties of cultured tobacco cells. Acta Biochim Biophys Sin (Shanghai). 1999;15:579–583.

23. Wang BC, Zhao HC, Wang XJ. Influence of sound stimulation on plasma-membrane H-ATPase activity. *Colloids Surf B Biointerfaces*. 2002b;25:183–188. doi:10.1016/S0927-7765(01)00320-4.
24. Hongbo S, Biao L, Bochu W, Kun T, Yilong L. A study on differentially expressed gene screening of *Chrysanthemum* plants under sound stress. *C R Biol*. 2008;331(5):329–333. doi:10.1016/j.crv.2008.02.007.
25. Mishra RC, Ghosh R, Bae H. Plant acoustics: in the search of a sound mechanism for sound signaling in plants. *J Exp Bot*. 2016;67(15):4483–4494. doi:10.1093/jxb/erw235.
26. Qin Y-C, Lee W-C, Choi Y-C, Kim T-W. Biochemical and physiological changes in plants as a result of different sonic exposures. *Ultrasonics*. 2003;41(5):407–411. doi:10.1016/S0041-624X(03)00103-3.
27. Cai W, He H, Zhu S, Wang N. Biological effect of audible sound control on mung bean (*Vigna radiate*). Hindawi Publishing Corporation, BioMed Research International; 2014. doi:10.1155/2014/931740.
28. Vicient CM. The effect of frequency specific sound signals on the germination of maize seeds. *BMC Res Notes*. 2017;10(1):323. doi:10.1186/s13104-017-2643-4.
29. Choi B, Ghosh R, Gururani MA, Shanmugam G, Jeon J, Kim J, Park S-C, Jeong M-J, Han K-H, Bae D-W, et al. Positive regulatory role of sound vibration treatment in *Arabidopsis thaliana* against *Botrytis cinerea* infection. *Sci Rep*. 2017;7(1):2527. doi:10.1038/s41598-017-02556-9.
30. López-Ribera I, Vicient CM. Drought tolerance induced by sound in *Arabidopsis* plants. *Plant Signal Behav*. 2017;12(10):10. doi:10.1080/15592324.2017.1368938.
31. De Luca PA, Vallejo-Marin M. What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Curr Opin Plant Biol*. 2013;16(4):429–435. doi:10.1016/j.pbi.2013.05.002.
32. Schöner MG, Simon R, Schöner CR. Acoustic communication in plant–animal interactions. *Curr Opin Plant Biol*. 2016;32:88–95. doi:10.1016/j.pbi.2016.06.011.
33. Brodie J, Lewis J, Ed. Unravelling the algae: the past, present, and future of algal systematics. *Syst Assoc Special Vol Series*. Boca Raton: CRC Press; 2007;75.
34. Frenkel J, Vyverman W, Pohner G. Pheromone signaling during sexual reproduction in algae. *Plant J*. 2014;79(4):632–644. doi:10.1111/tpj.12496.
35. Schwartz ER, Poulin RX, Mojib N, Kubanek J. Chemical ecology of marine plankton. *Natural Product Reports*. 2016;33(7):843–860. doi:10.1039/C6NP00015K.
36. Freeman SE, Freeman LA, Giorli G, Haas AF, Radford CA. Photosynthesis by marine algae produces sound, contributing to the daytime soundscape on coral reefs. *PLoS ONE*. 2018;13(10):e0201766. doi:10.1371/journal.pone.0201766.
37. Zinin PV, Allen JS, Levin VM. Mechanical resonances of bacteria cells. *Phy Rev*. 2005;72.
38. Apodaca G. Modulation of membrane traffic by mechanical stimuli. *Am J Physiol Renal Physiol*. 2002;282:F179–F190. doi:10.1152/ajprenal.2002.282.2.F179.
39. Hamant O, Haswell ES. Life behind the wall: sensing mechanical cues in plants. *BioMed Central Biol*. 2017;15:59. doi:10.1186/s12915-017-0403-5.
40. Sparke M-A, Wünsche J-N. Mechanosensing of plants. In: Warrington I, editor. *Horticultural Reviews*; 2020. doi:10.1002/9781119625407.ch2.
41. Ingber DE. Cellular mechanotransduction: putting all the pieces together again. *The FASEB Journal*. 2006;20(7):811–827. doi:10.1096/fj.05-5424rev.
42. Jiang R, Chen L, Li. Effects of sonic waves at different frequencies on propagation of *Chlorella pyrenoidosa*. *Agric Sci Technol*. 2012;13:2197–2201.
43. Cai W, Dunford NT, Wang N, Zhu S, He H. Audible sound treatment of the microalgae *Picochlorum oklahomensis* for enhancing biomass productivity. *Bioresour Technol*. 2016;202:226–230. doi:10.1016/j.biortech.2015.12.019.
44. Larsen P, Gilbert J, Ravasi T. Microbial Bebop: creating music from complex dynamics in microbial ecology. *PLoS ONE*. 2013;8(3):e58119. doi:10.1371/journal.pone.0058119.
45. Christwardana M, Hadiyanto H. The effects of audible sound for enhancing the growth rate of microalgae *Haematococcus pluvialis* in vegetative stage. *HAYATI J Biosci*. 2017;24(3):149–155. doi:10.1016/j.hjb.2017.08.009.
46. Golub N, Levturn I. Impact of sound irradiation on *Chlorella vulgaris* cell metabolism. *Eastern-Eur J Enterprise Technol*. 2016;2(10(80)):27. doi:10.15587/1729-4061.2016.63730.
47. Qi L, Teng G, Hou T, Zhu B, Liu X. Influence of sound wave stimulation on the growth of strawberry in sunlight greenhouse. *Int Fed Inform Proces*. 2010;317:449–454.
48. Hou TZ, Mooneyham RE. Applied studies of plant meridian system: I. *Am J Chinese Med*. 1999a;27:1–10.
49. Hou TZ, Mooneyham RE. Applied studies of the plant meridian system: II. Agri-wave technology increases the yield and quality of spinach and lettuce and enhances the disease resistant properties of spinach. Agri-wave technology increases the yield and quality of spinach and lettuce and enhances the disease resistant properties of spinach. *Am J Chin Med*. 1999b;27:131–141.
50. Abdullah NAH, Rani KA, Rahiman MHF, Noor AM. The effect of acoustic exposure on the growth of Mung Beans (*Vigna Radiata*). *Pertanika J Sci Technol*. 2019;27:1459–1470.
51. Altuntas O, Ozkurt H. The assessment of tomato fruit quality parameters under different sound waves. *J Food Sci Technol*. 2019;56(4):2186–2194. doi:10.1007/s13197-019-03701-0.
52. Ghosh R, Mishra RC, Choi B, Kwon YS, Bae DW, Park S-C, Jeong M-J, Bae H. Exposure to sound vibrations lead to transcriptomic, proteomic and hormonal changes in *Arabidopsis*. *Sci Rep*. 2016;6(1):33370. doi:10.1038/srep33370.
53. Kwon YS, Jeong M-J, Cha J, Jeong SW, Park S-C, Shin SC, Chung WS, Bae H, Bae D-W. Comparative proteomic analysis of plant responses to sound waves in *Arabidopsis*. *J Plant Biotechnol*. 2012;39(4):261–272. doi:10.5010/JPB.2012.39.4.261.
54. Bochu W, Jiping S, Biao L, Jie L, Chuanren D. Soundwave stimulation triggers the content change of the endogenous hormone of the *Chrysanthemum* mature callus. *Colloids and Surfaces B: Biointerfaces*. 2004;37(3–4):107–112. doi:10.1016/j.colsurfb.2004.03.004.
55. Yi J, Bochu W, Xiujian W, Daohong W, Chuanren D, Toyama T, Sakanishi A. Effect of sound wave on the metabolism of *Chrysanthemum* roots. *Colloids Surf B Biointerf*. 2003;29:115–118. doi:10.1016/S0927-7765(02)00155-8.
56. Gagliano M, Mancuso S, Robert D. Towards understanding plant bioacoustics. *Trends Plant Sci*. 2012;17:323–325.
57. Gagliano M, Grimonprez M, Deczynski M, Renton M. Tuned in: plant roots use sound to locate water. *Oecologia*. 2017;184(1):151–160. doi:10.1007/s00442-017-3862-z.
58. Jeong M-J, Shim C-K, Lee J-O, Kwon H-B, Kim Y-H, Lee S-K, Byun M-O, Park S-C. Plant gene responses to frequency-specific sound signals. *Mol Breed*. 2008;21(2):217–226. doi:10.1007/s11032-007-9122-x.
59. Jeong M-J, Cho J-I, Park S-H, Kim K-H, Lee SK, Kwon T-R, Park S-C, Siddiqui ZS. Sound frequencies induce drought tolerance in rice plant. *Pak J Bot*. 2014;46:2015–2020.
60. Kim J-Y, Lee J-S, Kwon T-R, Lee S-I, Kim J-A, Lee G-M, Park S-C, Jeong M-J. Sound waves delay tomato fruit ripening by negatively regulating ethylene biosynthesis and signaling genes. *Postharvest Biol Technol*. 2015;110:43–50. doi:10.1016/j.postharvbio.2015.07.015.
61. Banerjee S, Goswami A, Datta A, Pyne A, Nikhat A, Ghosh B. Effect of Different Sound Frequencies on the Growth and Antibiotic Susceptibility of *Escherichia coli*. *Int J Curr Microbiol Appl Sci*. 2018;7(3):1931–1939. doi:10.20546/ijcmas.2018.703.229.
62. Aggio RBM, Obolonkin V, Villas-Bôas SG. Sonic vibration affects the metabolism of yeast cells growing in liquid culture: a metabolomic

- study. *Metabolomics*. 2012;8(4):670–678. doi:10.1007/s11306-011-0360-x.
63. Ankur P, Sangeetha S, Seema N. Effect of Sound on the Growth of Plant: plants Pick Up the Vibrations. *Asian J Plant Sci Res*. 2016;6:6–9.
64. El-Rahman FA. Insight into the Effect of Types of Sound on Growth, Oil and Leaf Pigments of *Salvia officinalis*, L Plants. *Life Sci J*. 2017;14:4–8.
65. Chuanren D, Bochu W, Wanqian L, Jing C, Jie L, Huan Z. Effect of chemical and physical factors to improve the germination rate of *Echinacea angustifolia* seeds. *Colloids Surf B Biointerf*. 2004;37(3–4):101–105. doi:10.1016/j.colsurfb.2004.07.003.
66. Kim JY, Kim SK, Jung J, Jeong MJ, Ryu CM. Exploring the sound-modulated delay in tomato ripening through expression analysis of coding and non-coding RNAs. *Ann Bot*. 2018;122(7):1231–1244. doi:10.1093/aob/mcy134.